ASEXUAL REPRODUCTION AND GENETIC POPULATION STRUCTURE IN THE COLONIZING SEA ANEMONE *HALIPLANELLA LUCIAE*

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The acontiate sea anemone *Haliplanella luciae* (Verrill), since its presumed origin on the Pacific coast of Asia (Stephenson, 1935), has become distributed throughout the Northern Hemisphere. Populations are known to occur in Japan, on the west coast of North America and on the East Coast from Maine to Florida, in the Gulf of Mexico, in the British Isles and Western Europe, in the Mediterranean Sea and Suez Canal, and in Malaysia. Detailed zoogeographic records and historical accounts of the spread of *H. luciae* can be found in Parker (1902), Uchida (1932), Stephenson (1935), Carlgren and Hedgpeth (1952), and Hand (1955b). The dispersal of the species has been effected through attachment to oysters shipped commercially (Verrill, 1898), ship bottoms (Stephenson, 1935), and seaweed (Williams, 1973a).

Local populations of *Haliplanella* are often ephemeral, showing a tendency to appear suddenly, flourish for a time, and then to disappear abruptly (see Stephenson, 1953). A noteworthy aspect of the biology of this actinian is its eurytolerant nature, individual specimens surviving intertidal exposure to high summer temperatures, encasement in ice in winter, and exposure to drastically reduced salinities (Verrill, 1898; Hausman, 1919; Miyawaki, 1951; Kiener, 1971; Shick, 1976). Populations of *H. luciae* thus exhibit the temporal and physiological characteristics of colonizing species.

Uchida (1932) has described four distinct morphs of the species based on color and stripe pattern, although other records and unpublished observations suggest that variation may be more continuous. Local populations may be exclusively of one morph or (especially in locations geographically close to the species' center of origin) a mixture of several (Ômori, 1895; Uchida, 1932; Hand, 1955b; Williams, 1973b). A variety of synonymns has been applied to the species. Furthermore, as might be expected in such a widespread species, physiological races (*sensu* Stauber, 1950) have been described in isolated localities (Williams, 1973b; Shick, 1976). For example, individuals in the population studied by Sassaman and Mangum (1970) in Virginia typically show reduced metabolic activity and encystment in mucus at 10° C and below, while individuals from Maine are cold-adapted, remaining expanded and active at 0° C and below (Shick, 1976). According to the acclimation criteria of Prosser (1957), the demonstration of positive thermal compensation of metabolic rate in the Maine population (Shick, 1976) and of inverse thermal acclimation in the Virginia population (Sassaman and Mangum, 1970), would indicate that the two populations represent genetically determined physiological races.

Despite the current proliferation of accounts of genetic variation in natural populations, the genetic structure of sea anemone populations has received little

attention. The few exceptions to this generalization are the studies of Francis (1973a, b; 1976), Cain (1974), Dunn (1975), Ottaway and Kirby (1975), and Hoffmann (1976). The theoretical foundations for genetic investigations of sea anemones have been laid by students of the genetics of plants, sessile organisms which, like anemones, possess alternative modes of sexual and asexual reproduction.

In a preliminary paper, Shick (1976) presents evidence that the large population of *Haliplanella* at Blue Hill Falls, Maine, is a single clone: all specimens are males; reproduction by longitudinal fission is commonly observed; and fixed heterozygosity at a "tetrazolium oxidase" locus exists. Using the criterion of sex, a monoclonal structure of the female population at Plymouth, England, and the male population at Wells, Norfolk, England (R. B. Williams, personal communication), as well as of the female population in Selangor, Malaysia (D. F. Dunn, California Academy of Sciences, personal communication), may be inferred. The added criterion of electrophoretic screening of isolated populations was employed in this study to investigate the generality of this phenomenon in the species.

Finally, to clarify the significance of asexual reproduction in colonizing new habitats and in maintaining locally adapted populations, population structure and geographic distribution of *Diadumene leucolena* Verrill was examined. This actinian, which is a member of the same subtribe (Acontiaria) as *H. luciae* (which itself was formerly placed in the genus *Diadumene*), is ecologically similar to and often sympatric with *Haliplanella,* but is strictly sexual in its reproduction.

Materials and Methods

Samples of *Haliplanella luciae* were collected from four sites on the United States Atlantic coast. Physical data for the habitat of the type 1 (12 orange stripes on a greenish-brown column) anemones from Blue Hill Falls, Maine (BHF), have been presented elsewhere (Shick, 1976). A population of type 3 (48 paired white stripes on a green column) individuals from the Barnstable town dock, Massachusetts (BTD), was sampled in June and August, 1976. Types 1 and 2 (nonstriped) *H. luciae* from the Florida State University Marine Laboratory at Turkey Point, Florida (TP), were provided by L. L. Minasian, Jr. in October, 1976.

At Charlestown Salt Pond, Rhode Island (CSP), all four of Uchida's (1932) morphological types are present. In addition to those types already described, three type 4 (combining characters of types 1 and 3) individuals were also seen, and two of these specimens were collected for electrophoretic analysis. Type 1 individuals were likewise very rare at this site on both collecting dates (April and June, 1976), while types 2 and 3 were extremely abundant.

Specimens of *Diadumene leucolena* were collected at Narrow River, Rhode Island, by W. R. Ellington in December, 1975, and by us in April and June, 1976. Narrow River presents a true estuarine situation, with salinities averaging 8 to 10‰ at low tide (Ellington, University of Vermont, personal communication), which is below the critical limit for acclimation in *H. luciae* (Miyawaki, 1951; Shick, 1976), but within the zone of tolerance of the more euryhaline *D. leucolena* (Pierce and Minasian, 1974).

In preparation for electrophoresis, whole anemones were homogenized in two volumes of 0.1 M phosphate buffer, pH 7.0, and centrifuged at $7000 \times g$ for 20

minutes at $0°C$. Horizontal starch gel electrophoresis of the supernatant was performed using 12.6% (W/V) gels. At least one individual from the BHF clone was included as an internal standard on each gel. The enzymes and their abbreviations, buffer systems, and stains are listed in Table I. All enzymes were electrophoresed in three buffer systems; those given are those which produced the best resolution. To complement the electrophoretic studies, the sex of most individual anemones was ascertained by microscopic examination of either fresh gonadal smears or of Bouin's-fixed and sectioned specimens.

RESULTS

The variable and invariable enzymes, and the populations of *Haliplanella* in which they were examined, are listed in Table I. Only four enzymes were found to be variable, although leucine aminopeptidase (buffer II, stain B) appeared to be, but resolution was usually too poor for scoring. All observed allozyme phenotypes are shown in Figure 1. Alleles at each locus are designated alphabetically according to electrophoretic mobility of their enzyme products, the fastest-moving band being designated "A." By convention, the observed phenotypes are assumed to reflect the genotypes of individual specimens.

The genotype of each population is shown in Table II. For any given population, the numbers in each column, besides representing the number of individuals scored for that enzyme, also indicate the genotype at that locus. For example,

TABLE I

Enzymes examined electrophoretically in populations of Haliplanella luciae. *Population abbreviations are given in text.*

	Buffer	Stain	Population examined
Variable enzymes			
Hexokinase (HK)	II	A	All
Isocitrate dehydrogenase (IDH)	I, III	B	All
Phosphoglucose isomerase (PGI)	II	B	All
"Tetrazolium oxidase" (TO)	III	C	All
Invariable enzymes			
Esterase	II	A	BHF
Fumarase	IV	A	BHF
Glutamate oxaloacetate transaminase	III	B	All
Malate dehydrogenase	I, IV	B	BHF, CSP Types 2, 3
Malic enzyme	I, IV	B	BHF
Phosphoglucomutase	II	B	BHF
Xanthine dehydrogenase	IV	B	BHF, CSP Types 2, 3

Buffers   I.   Tris-citrate, pH 7.0 (Shaw and Prasad, 1970)
          II.   Lithium hydroxide, pH 8.1 (Ridgway, Sherburne and Lewis, 1970)
         III.   Tris-borate, pH 8.6 (Markert and Faulhaber, 1965)
          IV.   Tris-citrate, pH 6.3 (Selander, Smith, Yang, Johnson and Gentry, 1971)

Stains   A.   Modified from Shaw and Prasad (1970)
          B.   Modified from Selander *et al.* (1971)
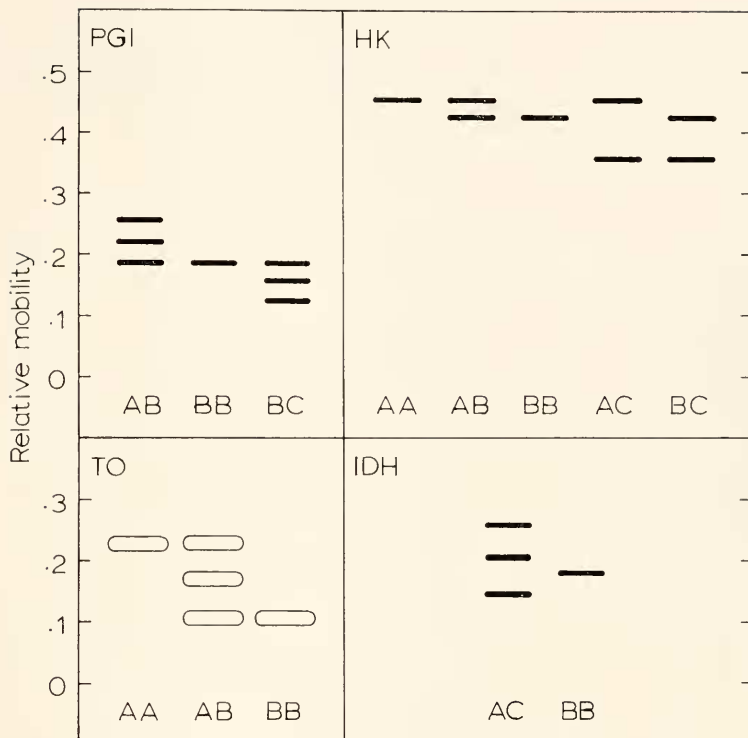   C.   Modified from Brewer (1970)

FIGURE 1. All phenotypic classes of allozymes at variable loci observed among populations of *Haliplanella luciae*. Mobilities are relative to bromphenol blue dye front. Anode is at top.

the genotype of all Blue Hill Falls individuals is: PGI- BB; TO- AB; IDH- BB; HK- BB, where 67 specimens were scored for PGI, 58 for TO, 31 for IDH, and 9 for HK. The numbers are different because some gels could not be reliably scored for every individual, and because some of the enzymes were found to be variable after the electrophoretic screening had begun.

All examined populations of *Haliplanella* appear to reproduce strictly asexually. In most cases this can be concluded from the incidence of fixed heterozygosity at one or more of the enzyme loci. In the cases of presumptive clone 1 of the type 1 anemones and of the type 4 specimens from Turkey Point, which are both homozygous at all loci, strict asexuality may be inferred from the sterile condition of the mesenteries. Although the possibility that these individuals may be sexually active during other seasons cannot be ruled out, their extremely small size would indicate that they are not sexually mature: there is an apparent body size threshold for gonadal maturation (D. F. Dunn, personal communication), and our casual observations of BHF individuals support this.

In the sexually reproducing *Diadumene leucolena*, only phosphoglucose isomerase (PGI) was found to be both variable and reliably scored. Results are presented in Table III. These data are pooled for the three collecting dates [G-test of independence (Sokal and Rohlf, 1969), $G = 2.034$, d.f. = 2, $0.5 > P > 0.1$],

TABLE II

Numbers of each genotype observed at four polymorphic enzyme loci in clonal Haliplanella luciae *from four Atlantic coast locations. Asterisks denote presumptive clones, which were homozygous at all loci examined.*

	PGI			TO			IDH		HK				
	AB	BB	BC	AA	AB	BB	AC	BB	AA	AB	BB	AC	BC
Blue Hill Falls, Maine													
Type 1 (male)	—	67	—	—	58	—	—	31	—	—	9	—	—
Barnstable town dock, Massachusetts													
Type 3 (sterile)	40	—	—	—	—	40	—	40	—	—	—	—	40
Charlestown Salt Pond, Rhode Island													
Type 1, clone #1 (sex not determined)	—	—	4	—	—	3	—	2	—	—	—	—	—
*Type 1, clone #2 (sex not determined)	—	4	—	3	—	—	—	—	—	—	—	—	—
Type 2 (male)	—	—	47	—	43	—	36	—	—	12	—	—	—
Type 3 (sex not determined)	—	32	—	—	23	—	—	21	—	—	—	—	3
*Type 4 (sex not determined)	—	2	—	—	—	—	—	2	—	—	—	—	—
Turkey Point, Florida													
*Type 1, clone #1 (sterile)	—	21	—	—	21	—	—	21	21	—	—	—	—
Type 1, clone #2 (sterile)	—	25	—	—	25	—	—	25	—	—	—	25	—
*Type 2 (sterile)	—	11	—	—	—	11	—	11	11	—	—	—	—

and there is no deviation from Hardy-Weinberg equilibrium (goodness of fit G-test for pooled data, $G = 4.190$, d.f. $= 3$, $0.5 > P > 0.1$). One individual heterozygous for the B allele and a rare allele product intermediate in electrophoretic mobility to the B and C allozymes was included with the BB individuals in the calculations.

DISCUSSION

Entire local populations of *Haliplanella luciae* commonly disappear suddenly, or individuals may become extremely rare. Numerous examples have been provided by Parker (1919), Allee (1923), Stephenson (1935), and in personal communications from the following persons at the indicated localities: B. L. Bayne (population near the Institute for Marine Environmental Research Laboratory at

TABLE III

Genotypic distributions and allele frequencies of phosphoglucose isomerase in Diadumene leucolena *from Narrow River, Rhode Island, including G-test analysis for goodness of fit to Hardy-Weinberg expectations. Expected numbers are given in parentheses.*

AA	AB	BB	AC	BC	CC	N	$G_{[3]}$
1 (0.16)	5 (6.19)	60 (60.05)	0 (0.50)	11 (9.71)	0 (0.39)	77	4.190, $0.5 > P > 0.1$

$f(A) = 0.046$; $f(B) = 0.883$; $f(C) = 0.071$.

Plymouth, England) ; D. F. Dunn (population of type 2 individuals in San Francisco Bay, California) ; C. P. Mangum (populations of type 1 and type 3 individuals at Indian Field Creek, Virginia) ; and our own observations (population studied by Sassaman and Mangum, 1970, at the Barnstable Town Dock, Massachusetts). As has been noted by Mayr (1963, p. 530) and Dobzhansky (1970, p. 249), such is a common fate of peripheral isolates or founder populations. The latter author comments that such populations represent the species at the limits of its ecological tolerance and may routinely be subjected to conditions beyond the tolerance limits.

The population at Blue Hill Falls, Maine, exemplifies the founder effect in the extreme—all of the anemones in an area of approximately 2000 square meters, in which the population density reaches 4000 individuals/m² (Shick, 1976), are members of a single clone. The consequences of a monoclonal population structure become evident upon examination of the results of the survival experiments presented in Shick (1976). Briefly summarizing these, *Haliplanella* shows 100% survival for two weeks at most temperature and salinity combinations from 1.0° C to 27.5° C and 0.5 to 35‰. However, a slight increase in the severity of conditions results in sudden extensive mortality: survival decreases from 95% at 22.5° C and 2.5‰ to 5% at 22.5° C and 1.0‰, and from 90% at 25.0° C and 2.5‰ to 0% at 27.5° C and 2.5‰. Thus, although *Haliplanella* is highly resistant to extremes of temperature and salinity, when the severity of conditions approaches the tolerance limits, there is an abrupt and massive incidence of mortality rather than a gradual elimination of individuals whose genotypes confer less resistance, since only a single genotype is present. Because other populations of this anemone typically are composed of one or a very few clones (Table II), the well known susceptibility of such populations to local extinction is not just understandable but even to be expected.

Factors other than temperature and salinity (*e.g.*, the biological factors of predation, competition, or disease) may also be involved in such local disappearances. We emphasize that the tolerance experiments above employed the criterion of survival for two weeks under stressful conditions, although salinities below 10‰ are ultimately lethal (see Shick, 1976).

The immense success of the BHF population is remarkable in that this location presents an extreme thermal environment (Shick, 1976) and is well beyond Salem, Massachusetts, the species' former known distributional limit on the North American Atlantic coast (Parker, 1919). This success is in large part due to the physiological adaptation to cold in the Maine individuals relative to members of more southern populations, an adaptation probably in existence before the species was introduced locally, in view of the short time involved. The species is not listed in Procter's (1933) survey of the region and was likely introduced in a shipment of oysters (*Crassostrea gigas*) imported from Japan and deposited in April, 1949, in Salt Pond, Sedgwick (Dow, 1970), the tidal outflow of which is Blue Hill Falls. A Japanese origin for this population is circumstantially supported by the much larger size (basal diameters of 1.5 to 2.0 centimeters being common) of these individuals relative to others on the Atlantic coast, and Hand (1955b) has remarked on the larger average size of Japanese specimens. Further, BHF individuals are now known to reproduce asexually by longitudinal fission and by constrictive pedal

laceration (Johnson and Shick, 1977), a situation hitherto unreported in populations outside Japan. Torrey and Mery (1904) and Stephenson (1929) deny the existence of more than one means of asexual reproduction in a given population, but it has in fact been recently observed in *H. luciae* from Shôbuta (Atoda, 1976).

Fertilization, and embryonic and larval development in the species remain to be described. *Haliplanella* is known to be dioecious, however, ripe male and female gonads having been seen in different populations; considering the high energetic cost of their production and maintenance (Chia, 1974; Giese and Pearse, 1974), they are presumably functional and adaptive in bisexual populations, which through chance have not yet been observed. The widespread occurrence of individuals having very small body size (see Stephenson, 1935; also, Barnstable Town Dock and Turkey Point, in the present study), typically a reflection of stress, and having sterile mesenteries rendering sex undeterminable (populations listed immediately above), supports the statement of Chia (1976) that asexual reproduction in sea anemones is favored under stressful conditions. Certainly a reproductive mode which obviates the necessity for nutrient-laden, costly-to-produce gonads, is much less expensive energetically.

More direct evidence for the absence of sexual reproduction in the mixed clonal populations at Charlestown Salt Pond and Turkey Point is provided by the observation that not all possible allelic combinations (expected in sexually reproducing populations containing heterozygotes) are present (Table II), unless there is total selection against the missing homozygotes. This does not imply that extreme selection does not occur in isolated *Haliplanella* populations; it may be significant that those in the two most physically rigorous habitats studied (BTD and BHF) are monoclonal, but it is not known whether this is the result of selection among several original clones at both sites or of the fortuitous introduction of single genotypes conferring predaptation to local conditions. The large differences in population size among the four morphological types present at CSP (Table II) may be indicative of the selective elimination of all genotypes but those best suited to that environment. The lack of success of the type 1 and type 4 anemones may not be entirely due to rigors of the physical environment, however, but perhaps also involves interclonal competition and aggression by the well-established type 2 and type 3 anemones that predominate at CSP.

The population at Barnstable Town Dock, which had a density of approximately 1000 individuals per square meter as recently as 1969 (Sassaman and Mangum, 1970), yielded only nine type 3 specimens from an area of 9 square meters during one hour of searching by us in June, 1976. Unfortunately, this population had not previously been characterized as to morphological type or genetic composition. Fixed heterozygosity at the PGI and HK loci (Table II) is good evidence that these nine individuals were members of one clone, which had become more abundant and widespread by August, 1976 (R. J. Hoffmann, University of Pittsburgh, personal communication; and Table II, for sample size). No specimens of *H. luciae* could be found at this site in July, 1977.

Asexual reproduction provides a mechanism for rapid colonization of a new environment through the production of multiple copies of a genotype which has proved to be successful under the local conditions. The continued success of specific populations of *Haliplanella* in the absence or near absence of genetic varia-

tion is undoubtedly a consequence of its eurytolerant nature (see Shick, 1976), an example of the "phenotypic plasticity" characteristic of colonizing species (Baker, 1965; Lewontin, 1965).

Baker (1965) has developed the concept of the "general purpose genotype" relative to weedy plants, in which there has been selection for a genotype or series of genotypes conferring broad environmental tolerance. This would allow an introduced species to build up a large population rapidly, without the loss of time involved in the selection of a unique, locally-adapted variant. This concept may also be applicable to populations of *Haliplanella luciae*, which present extreme cases of the founder effect, and which evidently rely on genotypes conferring the potential for successful physiological compensation over a wide range of environmental conditions at a given locality (*e.g.*, Blue Hill Falls). The eurytolerance of other clones reported in the literature, however, is likely not correlated with a single particular genotype, in view of the genetic diversity among clones reported in Table II.

Baker (1972) has observed that plant weeds, in which reliance on general purpose genotypes is common, are especially successful in habitats vacant of pests and competitors, and Selander and Hudson (1976) have suggested that the strategy of general purpose genotypes may fail where a colonizing species regularly co-occurs with genetically variable, rapidly evolving competitors, predators, and parasites. The highly successful BHF clone of *Haliplanella*, employing a suite of adaptations to extremes of temperature, salinity, and desiccation, monopolizes a habitat unoccupied by other locally occurring sea anemones. Both the epifaunal *Metridium senile* and the infaunal *Cerianthcopsis americanus* are present at this site, but exist subtidally or in the lowest reaches of the littoral where they are exposed only by spring low tides. Whereas subtidal populations of *Haliplanella* do occur (viz., CSP), the species at BHF is strictly intertidal, and the intertidal zone may represent a "refuge" for the anemone. Although there is no evidence of aggression by either *Metridium* or *Cerianthcopsis*, *Haliplanella* is heavily preyed on by the nudibranch *Aeolidia papillosa*, which is extremely abundant subtidally. This situation is reminiscent of that in *Mytilus californianus* on the Pacific Coast, where the mussel is restricted to the intertidal by subtidal populations of the predatory asteroid *Pisaster ochraceus* (Paine, 1974). An increased frequency of asexual reproduction under subtidal or low intertidal conditions (Johnson and Shick, 1977) may compensate for the heavy toll taken by the nudibranch and maintain a high population density down to mean low water.

In addition to those of producing multiple copies of successful genotypes and of offsetting losses due to predation, asexual reproduction also provides more immediate advantages manifested through living in dense aggregations (discussed for *Anthopleura elegantissima* by Francis, 1976): first, reduction of effective surface area, resulting in both diminished desiccation during intertidal exposure, and in reduced drag in wave-swept habitats; secondly, aggressive physical exclusion of interspecific and nonclonemate conspecific competitors; and thirdly, cooperation in food capture. Some of these may be important in *Haliplanella*, others less so.

Regarding the first point, increased longitudinal fission and a resultant aggregated spatial arrangement does not appear to occur preferentially under desiccating conditions in *Haliplanella*, since Uchida (1936) observed large, regularly-

striped individuals (indicative of minimal fission) in the *high* intertidal, and small, irregularly-striped (regenerating after fission) specimens *lower* in the intertidal. The maintenance of large individual body size would also serve to minimize surface area for evaporation (Ottaway, 1973). Laboratory experiments (Johnson and Shick, 1977) have shown that fission is less frequent, and individual body size and percentage water content larger, in *Haliplanella* experiencing variable, as opposed to continuous immersion, when feeding is equal. In the BHF population, desiccation resistance is also a result of microhabitat features, since the anemone occurs under rocks and among sand, gravel, and shell debris. Finally, the aggregation-related advantage of reduced drag does not appear to be important, since *Haliplanella* typically does not occur in unprotected wave-washed areas on the open coast (Stephenson, 1935; Hand, 1955b; Shick, unpublished observations).

Apropos of the second point, the only record of intraspecific aggression in *H. luciae* is for Japanese specimens reported in a review by R. B. Williams (1975), who discusses the aggressive function of catch tentacles. If the presence of catch tentacles is in fact indicative of aggression against nonclonemates (analogous to the function of acrorhagi in *A. elegantissima* described by Francis, 1973b; 1976), then the extreme rarity of their occurrance in *H. luciae* (Carlgren, 1929; Weill, 1934; both cited by R. B. Williams, 1975) indirectly supports the postulated generality of a monoclonal population structure in isolated colonies of this species. Indeed, the only population of *H. luciae* in which we have observed catch tentacles is the one at CSP, where all four of Uchida's morphological types are present, and the individuals in question were attached to an oyster clump containing both type 2 and type 3 specimens. *Haliplanella* has not been observed to use catch tentacles in interspecific aggression, however, and *Haliplanella, Diadumene,* and *Metridium* often coexist on the same rock.

Regarding cooperation in food capture, the third point raised by Francis, Hausman (1919) observed that single specimens of *Haliplanella* often failed to capture large beach fleas (*Orchestia*), but that the success rate was greater in aggregations of anemones where the tentacles of several contiguous anemones were brought to bear.

Selander and Hudson (1976), referring to work with plants and animals, emphasize that the understanding of the adaptive significance of different breeding systems must include consideration of a multitude of genetic and ecological factors. From the foregoing it is apparent that an understanding of asexual reproduction in sea anemones is enhanced by a detailed knowledge of the biology of the species in question. In a given population of *Haliplanella luciae,* the frequency and even the particular mode of asexual reproduction may be determined by an interacting network of physical and biological factors including temperature, exposure to desiccation, nutritional conditions, and pressure from competitors and predators. The anemone has both the physiological hardiness and the asexual potential for rapid colonization of extreme environments (*e.g.,* the Blue Hill Falls intertidal) uninhabitable by otherwise sympatric potential competitors and predators.

A comparison of *Haliplanella luciae* and *Diadumene leucolena* sheds further light on the evolution and consequences of sexual and asexual reproduction in sea anemones. The two species are sympatric over much of their range on the Atlantic coast of the United States, frequently occurring on the same rock. Both

species are notably euryhaline actinians and are similarly abundant in estuaries, and make a quantitatively identical use of free amino acids for cellular volume regulation (Pierce and Minasian, 1974; Shick, 1976). Populations of both species in Virginia are warm-adapted and show the comparatively rare pattern of inverse thermal acclimation of metabolic rate (Sassaman and Mangum, 1970).

Despite their similarities in Atlantic coast distribution and physiological responses to physical environmental factors, they are very different in their reproductive biology. Hand (1955b), based on the regularity of arrangement of the mesenteries, concludes that asexual reproduction does not occur in *Diadumene leucolena,* and our experience with living specimens supports this view. The conformity of genotypic frequencies in the Narrow River population to Hardy-Weinberg expectations (Table III) indicates that sexual reproduction is occurring there.

Evaluation of the proposed advantages of asexual reproduction may provide a clue concerning its absence in *D. leucolena.* The species is indigenous to the Middle Atlantic coast of the United States (Hand, 1955b), being especially common in sheltered estuarine habitats. It does not occur in wave-washed areas, and avoids desiccation in its typical microhabitats of empty barnacle tests and crevices among oyster clumps; thus, the twofold pressure to form asexual aggregations for surface area considerations is minimal. More important perhaps is the reduced competition with other native sea anemones for available hard substrate (an important consideration in epifaunal forms: Francis, 1976; Sebens, 1976), since the anemone fauna of the U. S. mid-Atlantic littoral is comparatively impoverished. This hypothesis is supported by the reproductive situation in other members of the genus *Diadumene* native to the U. S. Pacific coast, which has a diverse anemone fauna (Hand, 1955a, b): *D. franciscana* and *D. lighti* reproduce both sexually and asexually. Similarly, the British species *D. cincta* reproduces asexually, and the well-known diversity of the British sea anemones has been treated in the remarkable volumes of Gosse (1860) and Stephenson (1929, 1935).

Unlike monoclonal *H. luciae,* which shows a sudden and near total incidence of mortality as the tolerance limits for temperature and salinity are approached (Shick, 1976), the sexual maintenance of genetic variability in *D. leucolena* is reflected in a more gradual increase in mortality with increasing stress (Shick, unpublished). This is consistent with the proposal that sexual reproduction and genetic variability ensure population survival and promote evolution by reducing the likelihood of extinction (see G. C. Williams, 1975).

In August, 1976, the synchronous epidemic spawning of male and female *D. leucolena* occurred in a laboratory holding tank, and the previously unobserved embryonic and early larval development was followed. The light brown eggs (mean diameter 98 μm) adhered to the substrate at the bases of the spawning females, where they were fertilized by sperm released by the males. Fertilization success is no doubt enhanced by the eggs remaining *in situ,* rather than being broadcast into the water column. Early cleavage was symmetrical, and the blastula stage was achieved by 8 hours, and the planula larva stage by 12 hours, after fertilization at 17.5° C and 25‰. The planulae remained planktonic for at least five days.

Planktonic dispersal is especially important in an environment that is patchy with respect to available hard substrate. Epifaunal animals in the Chesapeake Bay sys-

tem (where *D. leucolena* is particularly abundant) are most prolific on subtidal oyster reefs, which are often separated by large expanses of soft bottom unsuitable for attachment by adults or settlement by metamorphosing larvae. Planktonic dispersal may thus assume the role of a means of colonizing new habitats, as well as maintaining good local recruitment (see Cory, 1967, and Sassaman and Mangum, 1970, for population size data). The greater success of *Haliplanella* as a colonizer (indicated by its occupation of a much wider geographic range and a greater variety of local habitats) is due not only to its ability to build up large populations quickly *via* asexual reproduction (*e.g.,* the resurgence of the species at BTD between June and August, 1976), but also to its eurytopic nature. While *Diadumene* is more restricted to hard, stable substrates, *Haliplanella* not only occupies rocks and oyster reefs, but also attaches to shell debris, gravel, and marine macrophytes such as *Ulva, Fucus, Zostera,* and *Ruppia.*

A limitation of sexually produced planktonic larvae as a colonizing mechanism [other than the obvious requisite presence of fertile individuals of both sexes, or of a fertile hermaphrodite (Dunn, 1975)] is that the range of environmental conditions permitting sexual reproduction is typically much narrower than that permitting mere survival. Thus, although *Diadumene leucolena* might survive introduction into a new environment, the ecological requirements for gametogenesis and spawning will not necessarily be met. If spawning should occur in an extreme environment, the intense selection predicted by G. C. Williams' (1975) models on animals with planktonically dispersed larvae would be even greater, presumably resulting in low local recruitment. Further, this strictly sexual anemone would have no prospect for the rapid intact preservation of the relatively few successful genetic combinations adapted to the immediate environmental conditions.

Intermediate to the two reproductive extremes presented by *D. leucolena* and populations of *H. luciae* studied to date is the condition exemplified by *Anthopleura elegantissima* and *Metridium senile.* The latter two species employ both sexual and asexual means of reproduction (for discussions and references, see Chia, 1976; Francis, 1976; Hoffmann, 1976). The availability of these alternatives allows for the ameiotic preservation of a proven successful genotype without sacrificing the genotypic plasticity provided by recombination through outcrossing. This situation is also likely the case in bisexual populations of *H. luciae,* which fortuitously have not yet been observed. Taken in their ecogenetic and evolutionary context, the present study and those of Francis (1976) and Hoffman (1976) support the reasonable conclusion that the optimum evolutionary potential involves a combination of sexual and asexual reproduction.

SUMMARY

Populations of *Haliplanella luciae* on the Atlantic coast of North America typically are composed of one or a few strictly asexual clones. The lack of genetic variability in one local population, that at Blue Hill Falls, Maine, is reflected in the population's response to extremes of temperature and salinity. As the limits of tolerance are approached, there is an abrupt and epidemic incidence of mortality, rather than a gradual one. Genetic and the concomitant physiological uniformity explain the well-known tendency for local populations of *Haliplanella* to disappear suddenly and illustrate a common outcome of the founder effect.

The success of *Haliplanella* as a colonizer is due to its extreme hardiness toward physical environmental factors and to its prolific asexual nature. Asexual reproduction by longitudinal fission and by pedal laceration not only provides a means of rapid colonization of a new habitat, but also a means of producing multiple copies of genotypes that have proved to be successful under local conditions. The resultant population structure recalls that in other animal and plant colonizers, in which there is heavy reliance on general purpose genotypes in isolated populations.

The comparative lack of colonizing success in the ecologically similar anemone, *Diadumene leucolena*, relates to its reproductive biology. Not only is the asexual potential for the rapid spread of successful genotypes lacking, but sexual reproduction typically requires a more optimal set of environmental circumstances which will not necessarily be met in a new habitat.

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